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Morphology of the Auditory Region in *Paramys copei* and Other Eocene Rodents from North America

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ABSTRACT

The morphology of the external surface of the petrosal and its junction with the basioccipital in *Paramys copei* is described. Comparison with an outgroup of the Cretaceous *Vincelestes* and Recent *Didelphis* and *Solenodon* reveals that the auditory region retains many primitive features. The Eocene paramyines from North America show only slight differences. *Sciuravus* is set apart by the lack of a ventral petrosal sinus canal between the petrosal and basioccipital and by the facial nerve and stapedial artery sharing a common foramen in the petrosal. European theridomyids, too, are not as primitive as *Paramys* but share with it and *Sciuravus* a ridge on the promontorium that separates the transpromontorial continuation of the internal carotid artery from the origin of the tensor tympani muscle. Twelve characters of the auditory region are analyzed and summarized in a data matrix for use in future studies. Relative primitiveness of the auditory region in all of these Eocene rodents suggests that derived characters in later rodent taxa may represent intraordinal relationships but only homoplasy with nonrodents.

INTRODUCTION

Rodent auditory regions are sufficiently known for some characters to be used in phylogenetic analyses. However, many visible structural details are not routinely described in publications on cranial anatomy. Thus, a wealth of additional characters exists that can be described and evaluated for polarity (primitive or derived). *Paramys* (family Ischyromyidae) is a key taxon in this category. It is

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one of the oldest fossil rodents in which sufficient detail has been preserved, and, in North American paleontology, the genus has been placed near the base of the rodent family tree as a kind of structural ancestor or example of primitiveness (Gregory, 1951: fig. 19.40; Wood, 1962: fig. 90). One expects it to be almost wholly primitive for rodents. Other contenders for structural primitiveness among rodents are the North American genus *Sciuravus,* which McKenna and Bell (1997: 186) put in a new and different suborder from the Ischyromyidae, and the European theridomyids (Lavocat and Parent, 1985: 338). Li et al. (1989) described the auditory region of *Cocomys,* a rodent from the early Eocene of China; future restudy of this specimen should yield important comparative details.

My primary purpose in this paper is to describe and illustrate the auditory region in *Paramys copei,* AMNH 4755 (holotype) and 4756. These two skulls preserve the finest detail that I have seen in any fossil rodent, and their early Eocene age, approximately 51 mya (million years ago), makes them important by antiquity. The rodent branch of mammalian phylogeny may have been separate already in Asia in the early Paleocene (*Heomys* Li, 1977); undisputed rodents are known from the late Paleocene: Alagomyidae in Asia and North America and Ischyromyidae in North America. In North America, the appearance of ischyromyid rodents defines the beginning of the Clarkforkian Mammal Age (Woodburne, 1987: 61) about 56 mya (McKenna and Bell, 1997: fig. 1). The early Eocene saw simultaneous diversification of rodents in Asia, North America and Europe. My second purpose is to compare the auditory region of *Paramys copei* with an outgroup of thoroughly described and illustrated mammals including the early mammal *Vincelestes,* the marsupial *Didelphis,* and the insectivore *Solenodon,* and with other Eocene rodents. My goals are to describe character polarities as a starting point for comparison of rodent auditory regions and to assess the relative primitiveness of *Paramys* auditory morphology.

The two specimens of *Paramys copei* were collected by Jacob L. Wortman in 1880 for Edward D. Cope. Images of the skulls have been independently illustrated and published: Cope, 1884, pl. 24a, figs. 1, 1a, 2, 2a; Wood, 1962, figs. 13 and 14; Wahlert, 1974, fig. 2. Similarly, independent versions of the auditory region have been published: Wood, 1962, fig. 14a; Wahlert, 1974, fig. 4; Parent, 1980, pl. 2, figs. 2, 4; Lavocat and Parent, 1985, fig. 1c. However, I found that there was still matrix obscuring morphology in the auditory region and even a matrix-covered petrosal displaced posterolaterally on AMNH 4755. To sit at a microscope and carefully use the sharpened tip of a thin beading needle to push away the fine covering matrix gives one an intimate feel for the shapes and edges as they are revealed. Identification of these features and comparisons with other living and extinct mammals were made from the literature mentioned below and from the ontogenetic studies by MacPhee (1981) and Wible (1984).

Among the first major comparative studies on auditory regions in mammals was that of van Kampen (1905), who built primarily on the fine German work in anatomy and development. Van der Klaauw (1931) made fossil mammals a part of his monograph; he was able to take advantage of the descriptions and collections of fossils from the American West that had accumulated since the late 1800s. Recent publications provide character analyses and detailed information about early mammals (Wible, 1990; Rougier et al., 1992; Wible and Hopson, 1993; Wible et al., 1995; Rougier et al., 1996; McKenna et al., 2000) and insectivores (McDowell, 1958; Novacek, 1986). The pioneering comparative studies on rodent auditory regions are relatively recent (Oaks, 1968; Parent, 1980; Lavocat and Parent, 1985). Many studies of living rodents have focused on taxa with inflated bullae (Webster, 1961, 1962, 1975; Pye, 1965; Webster and Webster, 1971, 1975, 1977, 1984; Lay, 1972, 1993; Wahlert, et al., 1993). Segall (1971) illustrated gliding and non-gliding sciurids. Information is also available about specific extinct taxa (Lavocat, 1967; Meng, 1990; Wahlert, 1974, 1977, 1978, 1983; Carrasco and Wahlert, 1999).

SPECIMENS EXAMINED

Specimens are listed according to the classification of McKenna and Bell (1997); generic assignments of paramyine species are

according to Korth (1984, 1985, and 1994). Abbreviations: **AMNH,** American Museum of Natural History; **USNM,** United States National Museum of Natural History.

Class Mammalia, Legion Cladotheria, Sublegion Zatheria, Family Vincelestidae

Vincelestes neuquenianus La Amarga Formation, early Cretaceous, Southern Neuquén Province, Argentina (information from Rougier et al., 1992)

Sublegion Zatheria, Supercohort Theria, Cohort Marsupialia, Magnorder Ameridelphia, Order Didelphimorphia, Family Didelphidae, Subfamily Didelphinae

Didelphis virginiana, AMNH 2070, Recent, no data.

Sublegion Zatheria, Supercohort Theria, Cohort Placentalia, Magnorder Epitheria, Superorder Preptotheria, Grandorder Lipotyphla, Order Soricomorpha

Solenodon paradoxus, AMNH 28270, Recent, Haiti

Sublegion Zatheria, Supercohort Theria, Grandorder Anagalida, Mirorder Simplicidentata, Order Rodentia. All specimens are of Eocene age.

Suborder Sciuromorpha, Family Ischyromyidae, Subfamily Paramyinae:

Tribe Paramyini

Paramys copei, AMNH 4755 (holotype) and 4756; Lost Cabin Member, late early Eocene, Wind River Formation, Wind River Basin, Wyoming; AMNH 103390, late early Eocene, San Jose Formation, San Juan Basin, New Mexico

Paramys delicatus, AMNH 12506 and 13090, Blacks Fork Member, middle Eocene, Bridger Formation, Bridger Basin, Wyoming

Notoparamys costilloi (type species) (= *Leptotomus costilloi*), AMNH 55110 and 55111 (holotype), Lost Cabin Member equivalent (Wind River Formation), late early Eocene, Huerfano Formation, Huerfano Basin, southeastern Colorado

Tribe Manitshini

Pseudotomus hians (type species), AMNH 5025 (holotype), Blacks Fork Member, middle Eocene, Bridger Formation, Bridger Basin, Wyoming

Pseudotomus petersoni (= *Ischyrotomus petersoni*) AMNH 2018 (holotype), Myton Member, late Eocene, Uinta Formation, Uinta Basin, Utah

Suborder Sciuravida, Family Sciuravidae

Sciuravus nitidus, AMNH 12531 and 12551, USNM 17683 and 22477, Blacks Fork Member, middle Eocene, Bridger Formation, Bridger Basin, Wyoming

AUDITORY REGION OF *PARAMYS COPEI*

The late early Eocene species *Paramys copei* (AMNH 4755, 4756, and 103390) preserves the most ancient, complete example of auditory region morphology that is available for rodents. I describe it below as a standard, and then note the differences of other Eocene rodent taxa. The region is illustrated in slightly oblique ventral view in figures 1, 2, and 3.

In ventral view the junction of the petrosal with the basioccipital is oblique, and the basioccipital is widest posteriorly. The anterior part of the basioccipital and adjacent basisphenoid appears swollen and may be pneumatized in the anterior portion. The posterior part is a flange that floors the ventral petrosal sinus. The posterior lacerate foramen is a lenticular gap medial to the posterior part of the auditory chamber and situated between the petrosal and the occipital. A broad ascending keel of the petrosal partly divides the anterior part of the gap, which transmitted the sigmoid sinus, from the posterior, for nerves IX, X, and XI. A prominent dimple in the petrosal just anterior to the keel is the opening of the cochlear canaliculus. A broad, covered passage between the basioccipital and the petrosal may mark the course of the ventral (inferior) petrosal sinus. It opens just anterior to the posterior lacerate foramen. The sigmoid sinus and ventral petrosal sinus joined here to form the internal jugular vein. A deep, horizontal flange of the basioccipital separates the ventral petrosal sinus from the brain (AMNH 4755, left side).

The petrosal ends anteriorly at the piriform fenestra; an anterior prong from the petrosal meets a posterior spine from the basisphenoid, and together they divide off the medial part of the fenestra as an anterior carotid foramen. The alisphenoid and possibly a narrow part of the squamosal form the rest of the anterior edge of the fenestra. The dorsolateral part of the petrosal abuts the squa-

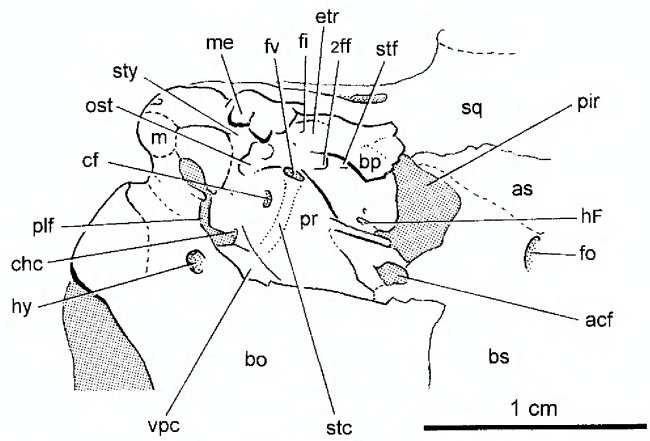

Fig. 1. *Paramys copei* (AMNH 4755) auditory region diagram with major features labeled; slightly oblique view of right auditory region; anterior is to the right. Abbreviations: **2ff** secondary facial foramen; **acf** anterior carotid foramen; **as** alisphenoid; **bo** basioccipital; **bp** bullar process of petrosal; **bs** basisphenoid; **cf** cochlear fossula; **chc** cochlear canaliculus; **etr** epitympanic recess; **fi** fossa incudis; **fo** foramen ovale; **fv** fenestra vestibuli; **hF** hiatus Fallopii; **hy** hypoglossal foramen; **m** mastoid; **me** mastoid eminence; **ost** fossa for origin of stapedius muscle; **pir** piriform fenestra; **plf** posterior lacerate foramen; **pr** promontorium; **sq** squamosal; **stc** stapedial artery channel; **stf** stapedial foramen; **sty** stylomastoid foramen; **vpc** ventral petrosal sinus canal at posterior lacerate foramen.

Fig. 2. *Paramys copei* right auditory region slightly oblique view.

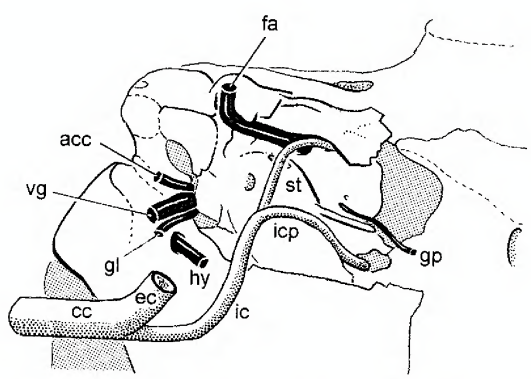

Fig. 3. *Paramys copei* right auditory region with arteries and nerves restored. Abbreviations: **acc** accessory nerve; **cc** common carotid artery; **ec** external carotid artery; **fa** facial nerve; **gl** glossopharyngeal nerve; **gp** greater petrosal nerve; **hy** hypoglossal nerve; **ic** internal carotid artery; **icp** transpromontorial continuation of internal carotid artery; **st** stapedial artery; **vg** vagus nerve.

mosal, and the mastoid, the posterior part of the petrosal, ascends and narrows to a point between the squamosal and occipital at the back of the skull.

The promontorium, which houses the cochlea, bulges anterolaterally. The fenestra vestibuli faces laterally; it is oval, about two times as long as wide, and the long axis is nearly horizontal. The cochlear fossula, which contains the fenestra cochleae, faces posteriorly. Dorsolateral to the promontorium, the roof of the tympanic cavity is domed as a fossa and bordered laterally by a tongue-shaped flange of the petrosal. Processes, canals, and basins permit one to reconstruct something of the nature of soft tissues.

The ventral surface of the promontorium bears evidence of the course of the internal carotid artery and its stapedial branch. The

internal carotid artery would have entered a posterior carotid foramen between the bulla and petrosal; it ran laterally, posterior to a change of surface angle that may mark the extent of bullar overlap, and then within a shallow groove that lies anteroventral to the cochlear fossula; finally it turned anteriorly, and the stapedial artery branched off. A deep gutterlike anterior sulcus on the promontorium may mark the transpromontorial course of the internal carotid artery. The sulcus is bounded laterally by a stout ridge; the ridge runs anteriorly from the middle of the lateral side of the promontorium. The origin of a moderately large tensor tympani muscle probably extended on the lateral surface of this ridge to the crest. A low swelling forms the medial side of the sulcus, and there is a hole anterior to the sulcus between the petrosal and the pterygoid region that is interpreted as the anterior carotid foramen. Evidence of the transpromontorial continuation of the internal carotid artery is stronger in *Sciuravus nitidus* (USNM 17683) (fig. 4); a shallow groove in a similarly situated sulcus joins the transverse groove of the internal carotid (Wahlert, 1974: fig. 8).

The stapedial artery branched from the internal carotid and passed through the intercrural foramen of the stapes (missing). The artery crossed below the facial nerve, ran anteriorly, above the medially projecting flange from the lateral tongue of the petrosal, and then entered the cranial cavity at the lateral side of the piriform fenestra. Temporal foramina, which are present in the squamosal-parietal suture and in the parietal, probably transmitted temporal branches from the superior ramus of the stapedial artery. In *Sciuravus nitidus* (AMNH 12531) a stapedial groove on the promontorium and an endocranial cast of the stapedial artery channel are visible (fig. 4). The artery divided into inferior and superior rami shortly after entering the cranium; the inferior ramus diverged anteriorly and the superior ramus dorsoanteriorly.

In ventral view the petrosal is very wide alongside the promontorium, and it is subdivided into two parts, a shallow median fossa that widens anteriorly and a complex lateral flange. The origin of the tensor tympani muscle occupied part of the fossa and extended ventromedially onto the ridge along the internal carotid sulcus. The bone that roofs the fossa alongside the promontorium may have been formed as the epitympanic wing of the petrosal (MacPhee, 1981: 52), a separate ossification from the tonguelike lateral flange. Schrenk (1989) found the fossa and lateral flange to be parts of a single structure in *Ctenodactylus*. The flange continues anteriorly from the crista parotica as does the embryonic tegmen tympani (Beer, 1985: 391). The considerable breadth and domed shape of the fossa and lateral flange suggest dorsolateral inflation of the auditory chamber.

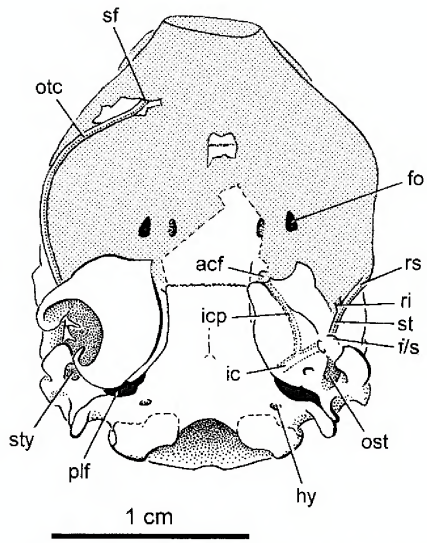

Fig. 4. *Sciuravus nitidus* (AMNH 12531) ventral view diagram of auditory regions and endocranial cast (with mechanical dot pattern). Anterior is toward the top of the page. Abbreviations: **acf** anterior carotid foramen; **fo** foramen ovale; **f/s** foramen shared by facial nerve and stapedial artery; **hy** hypoglossal foramen; **ic** internal carotid artery channel; **icp** transpromontorial internal carotid artery channel; **ost** fossa for origin of stapedius muscle; **otc** orbitotemporal canal (contained supraorbital branch of stapedial artery); **plf** posterior lacerate foramen; **ri** ramus inferior of stapedial artery (cast); **rs** ramus superior of stapedial artery (cast); **sf** sphenofrontal foramen; **st** stapedial artery (cast); **sty** stylomastoid foramen.

Dorsolateral to the anterior end of the fenestra vestibuli, the facial nerve emerged from the fallopian canal into the middle ear through the posteriorly facing secondary fa-

cial foramen at the posterior end of the fossa. The nerve ran posteriorly in the facial sulcus with the crista parotica on its lateral side; then it turned ventrally, where it was accommodated in a broad groove on the medial side of the mastoid eminence. It emerged from a probably incomplete or primitive stylomastoid foramen. A small canal for the major (greater) petrosal nerve diverges from the fallopian canal and passes through the roof of the fossa; it ends at an anteriorly directed foramen, the hiatus Fallopii, and is continued by a groove to the anterior edge of the petrosal at the piriform fenestra. The canal is exposed in AMNH 4756 by damage; it is widest near the facial nerve as would be expected, since it marks the branching of the major petrosal nerve from the geniculate ganglion.

The nearly vertical outer surface of the lateral flange of the petrosal was probably exposed between the squamosal bone and the tympanic bulla (missing). The flange forms an anteroposterior arch lateral to the fenestra vestibuli. Its ventrally facing surface contains a shallow, anteroposteriorly elongated basin, the epitympanic recess. Just posterior to the recess the fossa incudis is indicated by a slight pocket in the anterior surface of the mastoid eminence.

The stapedius muscle arose posterolateral to the promontorium in a basin within the ring of the lateral semicircular canal. The anterior boundary of the basin is formed by the ridge enclosing the lateral semicircular canal; the ridge extends from above the posterior end of the fenestra vestibuli to the mastoid eminence. The canal passes posteromedially around the depression for muscle origin and then through the robust bridge from mastoid to the promontorium. If the bulla in paramyines was similar to that in *Sciuravus* (Dawson, 1961: pl. 3; Wahlert, 1974: fig. 7) its bony posterior crus did not entirely cover this area, although the membrane that enclosed the chamber may have extended much farther posteriorly.

In ventral view there is a triangular depression in the mastoid posterior to the stapedius basin. The base of the triangle extends from the vertically projecting mastoid eminence medially to the posterior end of the posterior lacerate foramen. The apex of the triangle is at the paroccipital process, which is formed by the occipital bone and buttressed by the mastoid at its base. Novacek (1986: fig. 20) labeled a similar feature in *Leptictis* as the sulcus for origin of the digastric muscle. There are no mastoid cavities. The posterolateral extension of the mastoid contains a large chamber that housed the paraflocculus of the cerebellum; the smooth infilling of this chamber is exposed in AMNH 4755. The tympanohyal is presumed to be fused to the crista parotica.

The auditory chamber in all rodents is enclosed by the petrosal and ectotympanic; there is no participation by the squamosal or other elements in its wall. Traces of the auditory bullae can be found in a few fossil specimens; bullae are not preserved in *Paramys* and most of its Bridgerian (middle Eocene) relatives. The anteromedial part of the promontorium bears a broad facet in *Paramys.* The lateral margin of this facet is a low swell along the edge of the sulcus for the anterior continuation of the internal carotid artery; its posterior margin is formed by a change in surface angle that is just anterior to the channel for the internal carotid channel. The facet approximately matches the area where the dorsomedial curve of the bulla overlaps the promontorium in *Reithroparamys* and *Sciuravus.* At the lateral side of the petrosal, the flange derived from the tegmen tympani bears a ventral facet or seat at its anterior end, presumably for articulation of the anterior crus of the ectotympanic.

ANALYSIS OF EAR CHARACTERS IN PARAMYINES AND OUTGROUPS

A summary of character states is presented in table 1. These data are presented as a starting point for future studies; they do not reveal any pattern of relationships within the rodents and, when processed with PAUP, give a simple comb structure to a clade of the paramyines and *Sciuravus.* Some characters are included simply because they are important if other groups of mammals or later rodents are included in a comparative study. Data for *Vincelestes* are are taken from Rougier, et al. (1992).

Character 1: **Anterior part of basioccipital and adjacent basisphenoid** in ventral

TABLE 1
Character States in Outgroup Mammals and Paramyine and Sciuavid Rodents

Vincelestes	?0000	00100	00
Didelphis	01010	30010	10
Solenodon	01100	00011	00
Paramys copei	12102	01120	00
Paramys delicatus	12102	11120	01
Notoparamys costilloi	?2?02	11120	0?
Pseudotomus hians	121??	?1?20	01
Pseudotomus petersoni	121??	11120	01
Sciuravus nitidus	03101	21120	01

view *are not swollen laterally and may meet in a flat surface* (0); *appear swollen laterally and may project ventrally* (1). I do not know the morphology of this area in *Vincelestes.* In *Didelphis* the middle of the basioccipital swells anteriorly to meet a similarly swollen basisphenoid, but there is no lateral swelling; a similar increase in thickness can also be observed internally. In *Solenodon* there is no lateral swelling, and the bones meet in a flat surface.

The lateral swellings present in paramyines are very different from the condition in *Didelphis.* In *Paramys copei* lateral swellings of the basioccipital begin at the anterior end of the posterior lacerate foramen as a floor under the ventral petrosal sinuses; the swellings expand anteriorly so there is only a medial trough separating the pair at the anterior end of the bone; this is continued anteriorly on the basisphenoid, and the relief flattens out at the level of the foramen ovale. The character is present in *P. delicatus,* but the swelling is not as broad. The junction of basioccipital and basisphenoid in *Paramys* appears in side view as a broadly obtuse, downward projecting angulation of the medial elements of the basicranium.

Swellings in *Pseudotomus hians* and *P. petersoni* begin posteriorly with a low boss somewhat anterior and medial to the anterior end of the posterior lacerate foramen; the swelling continues only as far as the basioccipital-basisphenoid suture. The basicranium is not angled in side view. Dorsoventral flattening of specimens of *Notoparamys costilloi* makes it impossible to evaluate the character. *Sciuravus* has a very slight, if any, anterior increase in breadth of the lateral ridges abutting the petrosal, and the junction of basioccipital and basisphenoid is primarily flat; *Sciuravus* also lacks the ventral petrosal sinus between these bones and the petrosal.

Character 2: **Ventral (inferior) petrosal sinus** *is transmitted by a canal (enclosed passage) in the petrosal* (0); *is transmitted by a partly shielded passage between the basioccipital and the petrosal, and a short basioccipital flange may be present* (1); *is transmitted by a canal that deeply grooves the side of the basioccipital, and the sinus is separated from the brain by a deep, horizontal flange of the basioccipital* (2); *is transmitted endocranially, and no canal is present between the basioccipital and the petrosal* (3). The venous sinus passes through a petrosal canal in *Vincelestes* (Rougier et al., 1996). Wible (1990: fig. 4) illustrated the ventral petrosal sinus in *Didelphis* as entering a canal anterior to the posterior lacerate foramen. In the adult specimen that I have on hand, the canal deeply indents the lateral side of the basioccipital and enters the cranium, as shown by Wible. McDowell (1958: 139) stated: "As in other lipotyphlan insectivores, the ventral petrosal sinus of *Nesophontes* and *Solenodon* is exposed ventrally, owing to the failure of the petrosal and basioccipital to form a suture beneath the sinus immediately anterior to the jugular (posterior lacerate) foramen. This exposure extends forward from the jugular foramen, with which it is continuous, approximately to the level of the basioccipital-basisphenoid suture." The medial edge of the petrosal forms a partial roof above the sinus canal.

In *Paramys copei* and *P. delicatus* there is a wedge-shaped gap between the basioccipital and petrosal for the ventral petrosal sinus. It is widest at the posterior lacerate foramen and narrows anteriorly. The channel between the two bones is separated from the braincase by a broad, long dorsal flange of the basioccipital. This same character is present in *Pseudotomus* and *Notoparamys.* Petrosals are missing from *Pseudotomus hians,* and the channel incises on the lateral face of the basioccipital; it bends sharply dorsal at about the anterior end of the petrosal. The sinus must have entered the cranium at the foramen that could also have been for passage of the transpromontorial continuation of the in-

ternal carotid artery (anterior carotid foramen). In *Sciuravus* the petrosal is closely appressed to the basioccipital, and there is no room for the ventral petrosal sinus between them.

Character 3: **Piriform fenestra** (= middle lacerate foramen of some authors) *is small and medial* (0); *is large, and prongs of the petrosal and pterygoid separate the anterior carotid foramen from the lateral part of the fenestra* (1). In *Vincelestes,* an aperture identified as the ventral opening of the cavum epiptericum may be the same, at least in part, as the piriform fenestra. In *Didelphis* it is a small opening at the tip of the petrosal, and the carotid foramen is anterior to it. It is large in *Solenodon,* paramyines, and *Sciuravus.*

I use the term, piriform fenestra, instead of middle lacerate foramen as in my previous publications, and I have used anterior carotid foramen as the name for the place where the transpromontorial continuation of the internal carotid artery enters the cranium. The piriform (also pyriform = pear shaped) fenestra is a name coined by McDowell (1958: 128) for the "large vacuity in the roof of the middle ear (corresponding to the area of origin of the tensor tympani) of the Soricidae and Solenodontidae." He restricted the use of foramen lacerum medium to the entrance of the carotid artery into the skull and pointed out, however, that Story (1951) applied the term in carnivores to the foramen for the large vein from the ventral petrosal sinus that drains to the pharyngeal and pterygoid plexuses (McDowell, 1958: 124). MacPhee (1981: 58) broadened the meaning of piriform fenestra "to include the large gap, seen in all fetal and a few adult mammals, that lies between the auditory capsule and its dorsal outgrowths (tegmen tympani, epitympanic wing of petrosal) on the one hand and the epitympanic wings of the sphenoid and squamosal on the other." Moore (1981: 41) said that "posterior to the ala is the middle lacerate foramen which lies close to the entrance of the internal carotid artery into the cranial cavity . . . . The extension of the basisphenoid posterior to the pituitary results in this bone totally enclosing the openings for the internal carotid arteries (as occurs in typical amphibians and reptiles as well as in monotremes, marsupials and some insectivores and bats) or helping partly to marginate these openings at the middle lacerate foramina (in more advanced eutherians)" (ibid.: 56). Separate nameable foramina in this region have been partitioned off from the piriform fenestra by changes in the extent of bones.

In *Solenodon,* the hiatus Fallopii is in the anterior edge of the petrosal at the fenestra, whereas in paramyines it is in the middle of the fossa for the muscle origin. This suggests that the petrosal does not extend as far anteriorly in *Solenodon* as it does in rodents; the piriform fenestra in rodents may be created by failure of the alisphenoid and adjacent basisphenoid to grow posteriorly rather than of the petrosal to extend anteriorly. Another explanation is that in rodents the anterior part of the fossa for muscle origin does not descend far enough (that is, it slopes too steeply) to enclose the entire course of the nerve.

Character 4: **Internal carotid artery** *enters the middle ear, runs transversely, gives off the stapedial artery, and then turns anteriorly across the promontorium* (0); *does not enter the ear* (1). Rougier et al. (1992: fig. 3) reconstructed the internal carotid artery in *Vincelestes.* It ran laterally, gave off the stapedial artery, and then turned anteriorly in a channel on the anterior slope of the promontorium to the carotid foramen.

The internal carotid artery does not enter the ear in adult *Didelphis.* This is apparently a derived characteristic of marsupials. Concerning the morphology of the two isolated petrosals from late Cretaceous didelphoids, Wible concluded (1984: 310): "In particular, no vascular grooves appear on the ventral surface of the promontorium for either the internal carotid or stapedial arteries. This suggests that the medial position of the internal carotid and the loss of the stapedial artery are ancient traits among Marsupialia. Also, a large groove along the medial border of the petrosal's dorsal surface probably contained an intracranial ventral petrosal sinus." In conclusion about the living marsupials, Wible stated (1984: 312): "The internal carotid artery follows an extrabullar pathway medial to the tympanic cavity and promontorium of the petrosal . . . . The proximal sta-

pedial and its three branches, the posterior, superior, and inferior rami, are absent." The internal carotid artery enters the ear of *Solenodon*; it turns and continues anteromesially across the sloping anterior surface of the promontorium to the anterior border of the tympanic cavity. Its lateral branch, the stapedial artery, passes between the crura of the stapes and divides at the anterior edge of the petrosal into superior and inferior rami; the ramus superior passes through the posterolateral part of the piriform fenestra to become the middle meningeal artery within the cranium (McDowell, 1958: 140).

Paramyines and *Sciuravus* have a channel that runs transversely across the promontorium to the fenestra vestibuli; it indicates the presence of the stapedial artery. In *Sciuravus* a channel runs anteromedially from it on the anterior slope of the promontorium and represents the transpromontorial continuation of the internal carotid artery to the anterior carotid foramen. All paramyines have a large, gutterlike channel in this position that is bounded on the medial side by the abutment of the petrosal against the basioccipital and laterally by a crest that may have been part of the origin of the tensor tympani muscle. I have interpreted this morphology as evidence for the anterior continuation of the internal carotid artery within the ear. However, in paramyines the internal carotid does not mark the promontorium adjacent to the posterior lacerate foramen, and the stapedial channel is only clear close to the fenestra vestibuli; the arteries may not have touched the medial part of the promontorium. On the right side of one specimen of *Paramys delicatus* (AMNH 12506) I imagine that I see a faint, anteriorly running channel that ascends to the large anterior carotid foramen at the anteromedial end of the petrosal; it could be a channel for the internal carotid artery, and there seems to be adequate room for both an artery and the ventral petrosal sinus to pass through the foramen. However, this vague feature is not conclusive evidence of the artery.

Character 5: **Anterior part of the promontorium** *is smooth* (0); *has a low ridge that separates the course of the internal carotid artery from the fossa for origin of the tensor tympani muscle* (1); *has a prominent ridge instead of a low one* (2). The anterior slope of the promontorium is smooth in *Vincelestes, Didelphis,* and *Solenodon.* A prominent ridge is present in paramyines (no evidence is retained in *Pseudotomus*). It separates the fossa for origin of the tensor tympani muscle from a gutter that ascends anteriorly on the medial part of the promontorium. The ridge may have one or both of two functions: to delimit the channel for the anterior extension of the internal carotid artery, and to enlarge the site of origin of the tensor tympani muscle. *Sciuravus* (USNM 17683 and 22477, and Parent, 1980: pl. 3, fig. 3) has a slight ridge.

Character 6: **Stapedial artery** *is exposed in the middle ear along its entire course* (0); *enters a foramen anteroventral to the secondary facial foramen* (1); *enters an aperture together with the facial nerve and immediately passes laterally through a foramen into the cranium* (2); *is absent* (3). The stapedial artery is absent in *Didelphis.* The stapedial artery is exposed in the middle ear of *Vincelestes* and *Solenodon.* In *Vincelestes,* Rougier et al. (1992: fig 3) reconstructed the artery as splitting into a ramus superior that exits dorsally through the petrosal and an inferior branch that continues anteriorly in a channel. In *Solenodon* it branches into superior and inferior rami at the anterior end of the petrosal (McDowell, 1958: fig. 6).

In paramyines the stapedial artery is partly or entirely enclosed in a channel or canal that begins a short distance anterolateral to the intercrural foramen in the stapes. In *Paramys copei* it is partly covered by a medially projecting flange from the lateral tongue of the petrosal. It enters a foramen that is anterolateral to the secondary facial foramen in *Paramys delicatus, Pseudotomus petersoni,* and possibly *Notoparamys costilloi* (crushing makes character assessment uncertain). A specimen of *Sciuravus nitidus* (AMNH 12531) shows a complete picture of the arterial pattern. The basicranium and auditory regions are relatively intact, but the bone of the cranium is gone, and a clear endocranial cast remains. The stapedial artery passed through the intercrural foramen in the stapes (missing), turned anterolaterally into a foramen that also transmitted the facial nerve, and continued in an anterolateral direction

through the petrosal into the braincase. A cast of the course of the artery and its branches is visible on the left side of the endocranial cast (fig. 4). The inferior ramus diverged anteriorly just inside the cranium. The superior ramus continued laterally and then turned anteriorly; the course of the supraorbital branch in the orbitotemporal canal is marked by a cast that makes a broad arch that descends to the sphenofrontal foramen in a tiny bit of bone preserved in the back of the orbit; the artery was presumably accompanied by a vein.

Character 7: **Petrosal** *is narrow in width and length alongside the promontorium* (0); *is wide alongside the promontorium and the fossa in which the tensor tympani muscle arose, extends, and broadens anteriorly* (1). The fossa in which the tensor tympani muscle arose is narrow and long in *Vincelestes,* narrow and short in *Didelphis,* and narrow and tapered anteriorly alongside the promontorium in *Solenodon.* In paramyines and *Sciuravus* it is wide and broadens anteriorly as a shallow broad channel. The muscle origin leaves no distinct marks, so its actual extent in the fossa is not known with certainty.

Character 8: **Hiatus Fallopii** *is present in the medial part of the fossa in which the tensor tympani muscle arose* (0); *is present at the front edge of the petrosal fossa for the tensor tympani muscle* (1). In *Vincelestes* the hiatus Fallopii is in the fossa alongside the promontorium and not close to the anterior end of the bone. The hiatus Fallopii is present at the anterior edge of the petrosal in *Didelphis* and *Solenodon.* The hiatus Fallopii is in the medial part of the fossa for the tensor tympani muscle in *Paramys copei, P. delicatus, Pseudotomus petersoni, Notoparamys costilloi,* and *Sciuravus nitidus* (AMNH 12551, right side); the region is not preserved in *Pseudotomus hians.*

Character 9: **Petrosal exposure** in lateral view: *the petrosal is visible, supports the jaw joint, and contains the epitympanic recess* (0); *the dorsolateral edge of the petrosal is hidden by a downward overlap of the squamosal, the jaw joint is anterior and not directly supported by the petrosal, and the squamosal makes the lateral side of epitympanic recess* (1); *the dorsolateral part of the petrosal is exposed between the bulla and squamosal, the jaw joint is far anterior and not directly supported by the petrosal, and the epitympanic recess is entirely within the petrosal [the squamosal is grooved ventrally to receive the dorsal part of petrosal]* (2). The petrosal participates in the support of the glenoid fossa in *Vincelestes,* and it appears to be exposed in lateral view below the squamosal (Rougier et al., 1992: figs. 1, 2); the epitympanic recess is within the petrosal. The petrosal is hidden in lateral view by the squamosal in *Didelphis* and *Solenodon,* and the squamosal makes the lateral side of the epitympanic recess in both; I regard this as the primitive condition of the outgroup mammals. In paramyines and *Sciuravus* the dorsolateral part of the petrosal (the lateral flange) is exposed below the squamosal, and the epitympanic recess is entirely within the petrosal; this appears to be a different and derived condition compared to that in *Vincelestes,* in which the petrosal directly supports the jaw joint.

Character 10: **Epitympanic recess** *is a shallow channel* (0); *is deepened and enlarged* (1). *Vincelestes* and *Didelphis* have only shallow epitympanic recesses. The recess is slightly enlarged dorsally in *Solenodon.* The epitympanic recess is no more than a shallow groove in the lateral flange of the petrosal in all of the paramyines and *Sciuravus*; a slight pocket in the posterior end marks the fossa incudis.

Character 11: **Alisphenoid bone** *makes no part of the bulla* (0); *makes a part of the bulla* (1). The alisphenoid forms no part of a bulla in *Vincelestes.* A posteriorly concave process of the alisphenoid forms the anterior part of the bulla in *Didelphis.* The bulla in *Solenodon* is formed by a somewhat inflated but incomplete tympanic ring, and there is no contribution from the alisphenoid; the case is the same in paramyines and *Sciuravus.*

Character 12: **Shallow basin posterior to the crista interfenestralis (between the fenestra vestibuli and the fenestra cochleae)** *is simple and encircled by the lateral semicircular canal* (0); *is enlarged by a shallow depression that extends posteromedially from the basin ventral to the rim made by the lateral semicircular canal* (1). Some part of the basin is the fossa in which the stapedius muscle arises. In *Vincelestes* the basin

is immediately adjacent to the promontorium. The space posterior to the promontorium in *Didelphis* is short and deep; a slight depression in the posterior wall may mark the muscle origin. The basin is broad and shallow in *Solenodon*; a slight depression in the posterior side may mark the muscle origin. *Paramys copei* has a simple, deep basin. *Paramys delicatus* and *Sciuravus nitidus* (AMNH 12551) have a shallow posteromedial extension that is ventral to the semicircular canal. In *Pseudotomus* the extension appears to have been present, though all specimens are damaged. The region is crushed in *Notoparamys.*

DISCUSSION

The data matrix (table 1), when analyzed by PAUP, yields 56 trees of equal length (20 steps). The consensus tree shows the paramyines and *Sciuravus* as a clade with no internal resolution.

Comparison of the petrosals of *Paramys copei* and the early Cretaceous mammal *Vincelestes neuquenianus* (Rougier et al., 1992) is instructive in that there are many similarities in the correspondence of parts, but there are also structural differences and important differences in proportions. The shared primitive character states are: a low promontorium with grooves for both the internal carotid artery, which courses anteriorly across the promontorium, and its lateral branch, the stapedial artery; stapedial artery and facial nerve not sharing a common foramen; and epitympanic recess narrow and shallow and within the petrosal.

Vincelestes has features that are more primitive than the corresponding structures in *Paramys.* A large prootic canal, which encloses a part of the lateral head vein, is present in the petrosal lateral to the secondary facial foramen; the canal has been lost in placental mammals, except it is present in the basal eutherian *Prokennalestes* (Wible et al., 1997); the prootic sinus and lateral head vein disappear during early development in all eutherians, and venous drainage from the transverse sinus is via a new vessel, the capsuloparietal emissary vein, that exits from the skull at the postglenoid foramen (Wible, 1990: 192; Rougier et al., 1992: 202). The stapedial artery is exposed for its entire course in the middle ear, and it is not hidden by a flange as in *Paramys.* The promontorium lacks the anterior crest that in *Paramys* separates the channel for the promontory branch of the stapedial artery.

The most striking differences are in proportions and possibly stem from a radical change in stress-bearing function of the auditory region. In *Vincelestes* the glenoid fossa is immediately adjacent to the ear region, which therefore must be structurally integrated in the masticatory system. Monotremes retain the same arrangement, but in therian mammals, the jaw articulation is anterior to the auditory region (Rowe, 1988). In *Paramys* and all rodents and lagomorphs, the glenoid fossa is very far anterior, and the shape of the auditory region depends much more on the function of hearing, though the mastoid has an important role in attachment of neck muscles. The entire auditory region of *Paramys* is broad. The fossa alongside the promontorium that houses the origin of the tensor tympani muscle widens anteriorly, and there is a lateral flange with a ventral facet for supporting the anterodorsal part of the bulla. In addition, the mastoid extends posteriorly and makes an almost boxlike posteroventral corner of the skull. The lack of structural constraint from the masticatory system on the auditory region can be seen in the enlargement and elaboration of the bulla, the epitympanic recess, and the mastoid region in many different living and extinct rodents.

The insectivore *Solenodon paradoxus* (McDowell, 1958) retains some primitive features seen in *Vincelestes*: the promontorium is low and has a groove running anteromedially across the promontory for the internal carotid artery; the stapedial artery is exposed lateral to its passage through the stapes; and the epitympanic recess is narrow and shallow. But, like therian mammals, the prootic canal is lost, and a part of the venous drainage is via the postglenoid foramen, and the jaw articulation is anterior to the otic region. *Solenodon* has a large piriform fenestra that is covered with connective tissue and is the site of origin of the tensor tympani muscle (ibid.: 138–139). *Paramys,* the rest of the ischyromyids, and *Sciuravus* also have a

large piriform fenestra. In *Reithroparamys* (Meng, 1990: fig. 1; Wahlert, 1974: fig. 5), *Sciuravus,* theridomyids (Lavocat and Parent, 1985, fig. 1a), and many later rodents, the tympanic bulla covers at least the posterior part of the fenestra. Novacek (1985: 77) pointed out that rodents and lagomorphs share a uniquely enlarged piriform fenestra. In rodents this feature is anterior to the bulla and may represent reduction in ossification of the posteromedial end of the alisphenoid and perhaps of the adjoining basisphenoid that is in addition to reduction of the anterior part of the petrosal. I suspect that this reduction in ossification is possible in rodents and lagomorphs because the jaw articulation is is so far anterior. McDowell (1958: 137) attributed the fenestra in *Solenodon* to absence of the anterior part of the petrosal.

Wood (1962: fig. 3) and Wahlert (1974) identified a carotid canal between the basioccipital and petrosal of *Paramys delicatus,* but it probably housed the ventral petrosal sinus instead; a similar gap is visible in *Paramys copei* and in other paramyine genera. Wible (1984: 17) stated: "Wible (1983 [p. 286]) points out that the structure of the medial channels in the fossil basicrania is not always the same, but may be an open groove on the basioccipital-petrosal suture, a patent basicapsular fenestra (an open basioccipital-petrosal suture), or a closed canal between the basioccipital and petrosal. Of these three types of medial-channel morphology, only the first (the open groove) is ever associated with an internal carotid artery in extant eutherians, whereas venous sinuses are known to occupy channels of all three types." McDowell (1958: 139) described the condition in insectivores: "As in other lipotyphlan insectivores, the ventral petrosal sinus of *Nesophontes* and *Solenodon* is exposed ventrally, owing to the failure of the petrosal and basioccipital to form a suture beneath the sinus immediately anterior to the jugular (posterior lacerate) foramen. This exposure extends forward from the jugular foramen, with which it is continuous, approximately to the level of the basioccipital-basisphenoid suture." The anterior extent of the exposure is not so great in paramyines; the petrosal and basioccipital seem to be in continuous contact in *Sciuravus,* and the ventral petrosal sinus was endocranial; the auditory bullae obscure the character in Lavocat's (1967) illustrations of theridomyids.

Paramyines and *Sciuravus* share derived character states that are not present in the outgroup. These include the presence of a ridge on the anterior surface of the promontorium that separates the channel of the transpromontorial continuation of the internal carotid artery from the fossa for origin of the tensor tympani muscle. This fossa alongside the promontorium is wide and long with the hiatus Fallopii opening in its middle rather than in its anterior edge. The piriform fenestra is apparently formed by a decreased posterior extent of the ventromedial part of the alisphenoid and perhaps of the adjoining basisphenoid rather than decreased anterior extent of the petrosal as in *Solenodon.*

Paramys copei and the other fossil rodents examined also show an important derived feature of both rodents and lagomorphs: the squamosal does not participate in the wall of the epitympanic recess. Van der Klaauw (1931: 78–79) stated: "In the rodents we do not find the squamosal in the lateral wall of the epitympanic recess, but the petrotympanic. This small development of the caudal portion of the squamosal is a characteristic feature in rodents and causes the total absence of the squamosal in the walls of the tympanic cavity and its accessory cavities. As the tympanic and the petrosal are fused, it often can hardly be said which of the two forms the lateral wall of the epitympanic recess. Also the bony lateral wall can be totally absent. An incisura tympanica may be absent or present." He described lagomorph genera in the midst of the rodents and presumably considered them as part of the same group. The feature can be seen in Novacek's figure 4 (1985), which conveniently groups figures (after Kampen, 1905) of transverse sections of the mid-tympanic region in several mammals.

Lavocat and Parent (1985: 338) stated, "The most primitive rodent auditory region presently known by us is that of the Theridomorpha." They (ibid.: 336) proposed that the paramyines, in contrast to *Sciuravus* and the Theridomorpha, have a derived character that bars them from ancestry: "In *Sciuravus* and Theridomorpha, the auditory region is located at the very posterior part of the skull,

and the stapedius muscle, according to the shape of its insertion, was extending out of the tympanic cavity onto the surface of the posterior region of the skull, in the same manner as in many Recent Myomorpha, some archaic Insectivora (*Echinosorex, Erinaceus, Tenrec*), or *Tupaia.* In contrast, Paramyinae and *Franimys* show a very long horizontal mastoid exposed on the ventral part of the skull. This mastoid separates the tympanic cavity from the posterior part of the skull, while the pit of insertion for the stapedius muscle, being more vertical, results in the fact that this muscle was certainly restricted to the inside of the bulla."

It is possible to assess the condition of exposure of the stapedius muscle origin in *Sciuravus,* because two specimens (USNM 22477 and AMNH 12531) preserve the bulla, which is an expanded U with the base anteromedial. Since the bulla is small and not inflated, the area around the stylomastoid foramen is uncovered, and presumably the origin of the stapedius muscle was uncovered also. However, auditory bullae have not been preserved in *Paramys,* and the character cannot be properly assessed. Large bullae are preserved in *Reithroparamys,* and here the region is covered ventrally (Meng, 1990), although the posterior ends of the bullae are missing. *Paramys* specimens, with well-preserved auditory regions, are not as dorsoventrally flattened (distorted) as are *Sciuravus* specimens. The character described by Lavocat and Parent may be one of posterior completeness of specimens, extent of the auditory bulla, and postdepositional distortion rather than of morphology. It is not clear whether they supposed the muscle origin to have reached into the shallower posteromedial extension from the basin. This would have changed the length and direction of the muscle.

The question of which rodent is the most primitive is not simple. The theridomyid and adelomyine specimens are from the Phosphorites of Quercy, which range in age from the late Eocene Robiacian into the Oligocene. They are younger than the examined specimens of paramyines and *Sciuravus. Paramys,* the Theridomorpha, and to a lesser degree *Sciuravus,* share a strong ridge leading anteriorly from the promontorium that creates a deep channel for the transpromontorial continuation of the internal carotid artery (Lavocat, 1967: pls. 1, 2; Parent, 1980: pl. 3, fig. 4; Lavocat and Parent, 1985: fig. 1a). Lavocat and Parent did not note the derived features in theridomyids that are lacking in *Paramys* and *Sciuravus* but that can be seen in Lavocat's (1967) figures. First, a partition anterior to the foramen vestibuli extends from the promontorium to the medial side of the lateral petrosal flange; the partition marks the head of the fossa for origin of the tensor tympani. Such a partition was illustrated by Carrasco and Wahlert (1999) in *Cricetops dormitor,* but it is lacking in paramyines and *Sciuravus.* Second, Lavocat (1967: 492) stated that the epitympanic recess "constitue une fosse ovale assez profonde," and Lavocat and Parent (1985: 334) said the recess is "dorsally excavated and enlarged." This morphology, shown in Lovocat's (1967) figures of adelomyine theridomyids, is derived relative to the morphology of *Paramys* and *Sciuravus.* However, Lavocat (ibid.: figs. 1 and 2) presented a stereo photograph of the ear region of a theridomyid of unknown species. In it one can see a shallow epitympanic recess as in *Paramys* and *Sciuravus.*

The relationship of theridomyids to other rodents is unclear. Vianey-Liaud (1985: 293–294) summarized the data supporting descent from either the primitive Asiatic ctenodactyloids or the European ischyromyid stock. Martin (1999) showed that all of the early theridomyids have primitive pauciserial enamel as do the early ctenodactyloids and ischyromyoids; they could be descended from either stock. He defined and described pseudo-multiserial enamel in Oligocene theridomyids that is different from multiserial enamel in later ctenodactyloids and their descendents and thus is not evidence of relationship. The morphology of the auditory region of theridomyids is similar to that of paramyines and *Sciuravus,* but the bridge from the promontorium to the lateral petrosal flange, the enlarged epitympanic recess in some taxa, and the relatively large bulla are derived relative to the North American specimens. Knowledge of the ear region in early ctenodactyloids may help solve the problem of theridomyids origins.

In some features *Sciuravus* is more primitive than paramyines. *Sciuravus* lacks the lateral swelling of the basioccipital, and the ridge on the promontorium alongside the internal carotid artery is not as pronounced. However, *Sciuravus* possesses two characters that are derived relative to paramyines. There is no space between the basioccipital and petrosal for a horizontal ventral petrosal sinus. The distal part of the stapedial artery is not exposed; the artery and the facial nerve enter a common foramen and immediately diverge.

The morphological similarity of the auditory region in *Paramys copei* to the outgroup taxa reveals its primitiveness. The few derived characters mostly distinguish the genus as a rodent. In future comparative anatomical studies of rodent auditory regions, *Paramys copei* may be used as a standard of primitiveness. The fact that *Paramys, Sciuravus,* and theridomyids are all relatively primitive makes derived features shared among later rodents strong evidence of intraordinal relationship. Derived character states shared with nonrodents are thus independently derived and examples of homoplasy.

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